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Report

Sumatran Orangutans Differ in Their Cultural Knowledge but Not in Their Cognitive Abilities

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Summary

Animal cultures are controversial [1, 2] because the method used to isolate culture in animals aims at excluding genetic and environmental influences rather than demonstrating social learning [3, 4]. Here, we analyzed these factors in parallel in captivity to determine their influences on tool use. We exposed Sumatran orangutan (*Pongo abelii*) orphans from tool-using and non-tool-using regions (western swamps and eastern Langkat, respectively) that differed in both genetic [5] and cultural [6] backgrounds to a raking task and a honey-dipping task [7, 8] to assess their understanding of stick use. Orangutans from both regions were equally successful in raking; however, swamp orangutans were more successful than Langkat orangutans in honey dipping, where previously acquired knowledge was required. A larger analysis suggested that the Alas River could constitute a geographical barrier to the spread of this cultural trait [9]. Finally, honey-dipping individuals were on average less than 4 years old, but this behavior is not observed in the wild before 6 years of age. Our results suggest first that genetic differences between wild Sumatran populations cannot explain their differences in stick use; however, their performances in honey dipping support a cultural differentiation in stick knowledge. Second, the results suggest that the honey-dippers were too young when arriving at the quarantine center to have possibly mastered the behavior in the wild individually [10], suggesting that they arrived with preestablished mental representations of stick use or, simply put, "cultural ideas."

Results and Discussion

Culture in animals remains controversial [1, 2, 11]. The debate mainly revolves around whether the diversity of behaviors observed between communities in some species [3, 6, 12, 13] results from differences in what is socially learned by individuals in each community or from different genetic predispositions, developing in response to particular environments [1, 14, 15]. Recent studies have shown that environmental or genetic effects alone cannot explain all the observed variation, supporting a role for cultural transmission [4, 16–18]. Previous work with chimpanzees has also suggested that apes do not simply apply behaviors in response to environmental constraints, but that there is a fundamental cognitive basis to their cultural behaviors [8]. One reason why the debate continues is that it is particularly difficult to identify social learning in wild primates [19], although it is well demonstrated in captivity [20, 21] and notably in wild-born sanctuary orangutans [22]; however, no experiment thus far has proven that behaviors deemed cultural in the wild were transmitted socially, despite suggestive evidence [7, 23–25].

In this study, we wanted to assess whether the cognitive abilities of recently rescued rehabilitant Sumatran orangutans (*Pongo abelii*) at a quarantine center in Sumatra differed substantially according to their cultural knowledge. For this, we designed two stick-based food-retrieval tasks: a food-raking task, for which individuals could choose between a hook and a stick to retrieve food positioned outside their cage, and a honey-dipping task previously used with wild chimpanzees [7]. The cognitive abilities playing a role in the learning and display of stick use, tested equally by our two tasks, are diverse. Animals must be morphologically able to use tools but also capable of a certain physical understanding of the object, and its use as a tool, to accomplish the task (physical cognition). Finally, subjects may rely on their innate abilities to learn from others (social cognition), a cognitive ability playing a key role in cultural transmission. All of these abilities are coded for in the first instance within the genome. The rationale we followed was that individuals that did not differ substantially in these cognitive abilities would likewise not differ in their results in cognitive tasks testing these abilities. Our choice of tasks, however, could potentially demonstrate a difference in cultural knowledge.

To test both the genetic and the cultural effects, we selected orangutans from two Sumatran regions constituting two genetically and culturally distinct populations: orangutans from the swamp populations (Tripa, Kluet, and Singkil), who use sticks to extract honey [26], and orangutans from the eastern coastal regions around Langkat, where tool use is almost certainly absent. In Langkat, direct observations of unsuccessful attempts by orangutans to extract honey from tree holes were made by one of us (C.v.S., unpublished data); additionally, a brief field study yielded no extractive tool use on tree holes or *Neesia* fruits (S.A. Wich, personal communication; [9]) Finally, no tools were collected during surveys [27]. Although this cannot prove that this population never uses tools, the presence of customary tool use in wild orangutans is related to orangutan density and opportunities for social learning [6]. Because the ecological settings and low densities of orangutans in Langkat parallel those found in Borneo [27], where no extractive tool use has been observed despite long-term research, it is highly likely that Langkat orangutans do not use tools to extract their food. A second incentive to compare these two populations was that they are genetically distinct [5], which allowed us to assess whether genetic predispositions could account for differences in stick use through the raking task.

The swamp and Langkat groups ($n_{swamp} = 13$, $n_{Langkat} = 10$; Table 1) did not differ in age distribution (Mann-Whitney [MW] U test, U = 82, p = 0.313), time spent in the rehabilitation center (MW test, U = 57, p = 0.648), or effective and possible time spent engaging with the honey device (MW test, U = 59.5,

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Table 1. Summary of Results in the Honey-Dipping and Raking Tasks for Individuals Tested at the Quarantine Center

Individual	Sex	District of Origin	Age (Years)	Time in Center (Years)	Honey-Dip Knowledge	Effective Time (s)	Possible Time (s)	Rake Knowledge
Swamps								
BO	M	Aceh Selatan	5.5	1.5	no	721	1,306	yes
BW[b]	F	Subulussalam	4.5	3	yes	171	401	no
CY[b]	F	Aceh Selatan	4.5	3	yes	267	267	yes
FR[b]	M	Singkil	4	2.5	yes	227	330	yes
JB	F	Nagan Raya	4	0	no	528	1,050	yes
LB[a]	F	Nagan Raya	3	0	no	138	480	yes
LU	F	Singkil	4.5	1.5	yes	147	282	yes
MK[b]	M	Nagan Raya	5	3	yes	520	715	no
MO	F	Nagan Raya	6.5	0.5	yes	24	24	yes
ON	M	Aceh Selatan	4	1	yes	450	492	yes
RM	M	Aceh Selatan	3.5	0.5	no	608	888	no
SE	M	Nagan Raya	9	2	yes	369	669	yes
UD	M	Nagan Raya	8	0	yes	29	29	yes
West Leuser								
EG	M	Aceh Tenggara	4.5	0.5	yes	51	126	yes
KA	F	Aceh Tenggara	3.5	0.5	no	180	647	no
RU	M	Gayo Lues	7.5	3.5	yes	114	114	yes
SC	F	Aceh Tenggara	5	1	yes	776	972	no
ST	F	Gayo Lues	3	1	no	373	1,110	no
WD	F	Gayo Lues	3.5	2.5	yes	340	452	no
YU[b]	F	Aceh Barat Daya	5	3	no	679	1,009	no
East Sumatra (including Langkat)								
BI	F	Aceh Tamiang	10.0	0	no	388	923	no
CM[a]	F	Aceh Tamiang	3.0	0	no	115	894	no
CP	M	Sumatera Utara	20	0	no	191	796	no
GK	F	Sumatera Utara	30.0	0	no	237	1,030	no
JK[b]	M	Langsa	4.5	2.5	no	390	1,077	no
PU[b]	F	Aceh Tamiang	4.5	2.5	yes	29	73	yes
RK[a]	M	Sumatera Utara	4.5	0.5	no	137	545	yes
SU	F	Sumatera Utara	3	1	no	465	900	no
TL	F	Sumatera Utara	10.5	8.5	yes	201	201	yes
TO[b]	M	Aceh Tamiang	5.5	2.5	no	765	900	yes
Undetermined								
BA	M	Aceh Tenggara	4.5	1	no	370	705	yes
JU	M	Aceh Tenggara	3.5	0.5	yes	159	204	yes
KI	M	Aceh Tenggara	4.5	1	no	387	973	no
MA	F	Aceh Tengah	8.5	2.5	yes	215	215	no
MV	M	Aceh Tenggara	4	0	yes	139	328	no
PK[b,c]	M	Gayo Lues	4.5	3	yes	225	300	yes

Results shown exclude individuals seized in main cities. Individuals are sorted according to their place of origin from west to east: swamps (Tripa, Nagan Raya; Kluet, Aceh Selatan; Singkil, Aceh Singkil, and Subulussalam), West Leuser (Aceh Barat Daya, Aceh Tenggara, and Gayo Lues), and East Sumatra (Langsa, Aceh Tamiang, and Sumatera Utara including Langkat). Knowledge of the techniques in the honey-dipping and raking tasks is given as yes/no, and effective time and possible time spent engaging with the log during the honey-dipping task are given in seconds (s).

[a]Individuals that reached the 167 s criterion in the subsequent learning experiment.

[b]Geographic origin confirmed by independent genetic analysis.

[c]Individual belonging to the Langkat population but seized in Aceh [28].

p = 0.738, and U = 89, p = 0.148, respectively). Our first prediction was that if orangutans differed in their cultural knowledge, orangutans from the swamp areas would be more likely to display honey dipping than Langkat orangutans. The distribution of honey-dipping knowledge was significantly different between the two groups (Fisher's exact test, p = 0.036; Figure 1A). Only 2 of 10 Langkat individuals (20%, PU and TL; TL had spent over 6 years in the center, long enough for possible enculturation) could extract honey from the device, compared to 9 of 13 swamp individuals (69%).

This difference could also potentially result from genetic differences, but then we would expect to find the same difference in the distribution of rake knowledge as in the honey-dipping task (our second prediction). However, this was not so: the distribution of rake use knowledge did not differ between the two groups (Fisher's exact test, p = 0.102; Figure 1B), as 4 of 10 Langkat individuals (40%) and 10 of 13 swamp individuals (77%) could rake food. Although our results may suggest that fewer Langkat orangutans than swamp orangutans succeeded in the raking task, another individual, PK, seized in Aceh (Table 1) but belonging to the Langkat genetic population and thus excluded from analysis for rearing history, also knew stick use, strengthening the idea that the genetic material of Langkat orangutans does not hinder their stick-using abilities. Because this result was nonetheless somewhat ambiguous, it was possible that there could be some effect of genetic factors or some transfer of knowledge between the two tasks. If either of these possibilities were

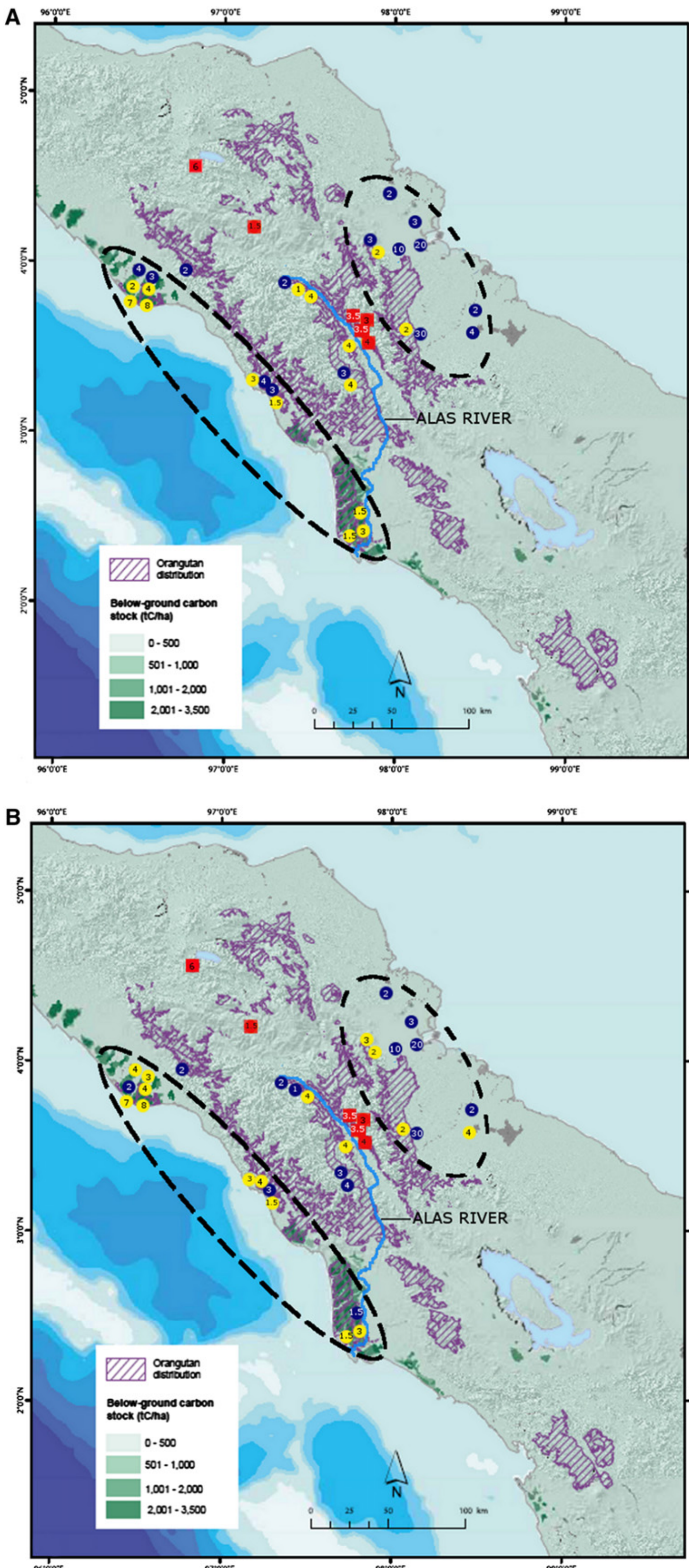

Figure 1. Map of a Northern Section of Sumatra Showing the Origins of the Tested Orangutans and Their Results in the Honey-Dipping and Raking Tasks

Yellow dots indicate “knowledgeable” individuals; blue dots indicate “ignorant” individuals. Numbers inside the dots are the age of arrival at the quarantine center of a given individual and are in black for knowledgeable individuals versus white for ignorant individuals. The blue line is the Alas River. The green gradient shows the below-ground carbon stock: darker regions correspond to the swamp areas. The elongated dashed circle indicates individuals belonging to the swamp population; the shorter dashed circle indicates individuals belonging to the Langkat population. Red squares indicate individuals that were excluded from the geographical analysis because they originated from a major city or could not be assigned to a population. Map adapted from [29] with permission of authors.
(A) Honey-dipping task.
(B) Raking task.

correct, success in the raking task should then predict success in the honey-dipping task. To control for this possibility, we ran a mixed model. Controlling for the confounding effects of orangutan characteristics (mixed model analysis; age, Wald Z = 0.501, p = 0.616; sex, df = 1, 15.772, F = 1.379, p = 0.258; age upon arrival at the center, Wald Z = 0.493, p = 0.622), success in the raking task did not predict success in the honey-dipping task (mixed model analysis; df = 1, 18.781, F = 0.981, p = 0.335). Only the origin of the orangutans predicted success in this task (mixed model analysis; df = 1, 17.384, F = 5.506, p = 0.031). This shows that neither a genetic explanation nor transfer of knowledge is likely to explain the results found in the honey-dipping task, making the cultural explanation the most likely one. Taken together, our results support the hypothesis that orangutans arrived at the quarantine center with different cultural knowledge, on which they relied to solve an experimental task, paralleling results obtained previously with wild chimpanzees [7].

Considering a larger sample of individuals, we found that honey dippers were not randomly distributed on both sides of Alas River but mostly originated from regions west of the river (Fisher's exact test, p = 0.050; Table 2). East of the river, only the two previously mentioned Langkat individuals (PU and TL) were found to fish for honey. In comparison, we did not find any differences in the distribution of rake users relative to the sides of Alas River (Fisher's exact test, p = 0.442; Table 2).

These results support the hypothesis that the Alas River constitutes a geographical barrier to the spread of the honey-dipping cultural variant. They also suggest that populations found in the Gayo Lues and Aceh Tenggara regions may know tool-based extractive techniques. This is not surprising, because other types of tool use have been recorded in these populations [6, 30]. Interestingly, these sites, located in the West Leuser region, support high orangutan densities, suggesting higher social learning opportunities [27]. However, some populations west of the river (e.g., Ketambe) have not been observed using tools for extractive purposes. This could explain why the difference found between the two groups, although still significant, was less strong than when including only swamp orangutans, where extractive tool use is customary [6].

Table 2. Summary of the Number of Knowledgeable and Ignorant Orangutans in the Two Tasks in Relation to the Alas River

Region	Knowledge	Honey Dipping	Raking
West Alas	knowledgeable	13	12
	Ignorant	7	8
East Alas	knowledgeable	2	4
	ignorant	8	6

Finally, excluding the two honey dippers from Langkat, we found that the West Alas individuals successful in the honey-dipping task arrived at the center at a mean age of 3.4 years (n = 13, range 1–8 years). This value did not differ from the mean age of 6.3 years at which non-honey dippers arrived (n = 15, range 2–30 years, MW test, U = 114, p = 0.467).

These age data suggest that most individuals who displayed the behavior were too young when they arrived at the center to have possibly experimented with this behavior in the wild. Infants at Suaq, a site with extensive extractive tool use, do not use tools before age 4 and do not feed independently using tools until age 6 or 7 [10]. In our sample, only 2 of 17 individuals may have reached this age before being separated from their mother. Because honey dippers were not older than the non-honey-dipping individuals at their arrival at the quarantine, an explanation based on a longer exposure to particular environmental conditions is unlikely. These observations thus suggest two alternative scenarios: either orangutans from different regions arrived at the center with different propensities to consider objects as tools, supporting a genetic explanation, or they arrived with different acquired knowledge, but this knowledge did not result from already well-developed and practiced behaviors. Our results in the raking task make the first scenario unlikely.

The second scenario, however, requires an explanation of how orangutans would arrive at the center with a knowledge they did not physically express. A possible answer to this problem is to consider that cultural knowledge has a deep cognitive basis and is found at the mental representation level of "ideas" [31]. Here, our data suggest that the tested orangutans differed in the "cultural ideas" they had been exposed to, and that they could have learned these ideas before being able to perform them. In contrast, individuals born in areas where stick use has not been recorded had probably not been exposed to the behavior, and thus failed to find a solution to the honey-dipping problem [8, 18]. In conclusion, our results support the hypothesis that culture in animals is cognitive, and that animal culture may be acquired at the representational level ("ideas") rather than the behavioral level.

Experimental Procedures

Subjects and Settings

The study was conducted in the Batu Mbelin Quarantine Center, Sibolangit, North Sumatra (3°19′42″N; 98°34′51″E), a center where confiscated wild-born orangutans are rehabilitated before release in undisturbed Sumatran forests. Ages were estimated at arrival through a combination of body size and teeth eruption status. Region of origin was acquired from records of the exact location where the orangutans were seized. Upon arrival at the center, rescued animals are housed first individually and then in large social groups (isolation phase and socialization phase, respectively; see Figures S1A and S1B available online). Tests were conducted individually with orangutans from both the isolation and socialization phases to increase sample size. The two tasks were proposed as "one-shot" experiments, where individuals were tested only once and for a time assumed to be too short for them to develop a solution on an ad hoc basis. Data were acquired between February 21 and March 16, 2012.

All orangutans tested came into the cage willingly and were allowed to engage with the apparatus after the keeper had installed the experimental setting. The procedures complied with the laws and regulations of the Republic of Indonesia and were reviewed and approved by the Indonesian Ministry of Research and Technology.

Tasks

Honey-Dipping Task

Orangutans were presented with a vertical wooden log with a hole 3 × 3 × 16 cm (length × width × depth) and a 40 cm wooden branch, stripped of its leaves along half of its length, the "leafy stick" [8]. Orangutans observed the keeper put 55 ml of honey into the hole and were then allowed to engage with the log. Individuals were given 10 min of possible engagement with the log. Individuals were considered "knowledgeable" of the honey-dipping technique if they inserted an object in the hole and "ignorant" if they did not. For this task, we measured the time that orangutans spent in immediate proximity to the log (direct interaction or less than 1 m away) ("effective time") and time next to the log while not engaging with it ("possible time"). The average effective and possible times before using a stick to dip for honey were 176 s and 249 s, respectively (n = 23, range 24–450 s and 24–669 s, respectively; unpublished data).

Raking Task

Orangutans were presented with a 40 cm stick and a 40 cm hook (a stick with an additional hook part) and an inaccessible food item outside their cage. Each individual was presented with a preferred food to avoid a lack of motivation. If the subjects remained unsuccessful through all trials, they were given the food item at the end to make sure they wanted the item. Orangutans were given three trials each for a total duration of 5 min. If the tested individual attempted to use a tool to obtain the food item, the individual was coded as knowledgeable; if not, they were considered ignorant.

All animals were exposed first to the honey-dipping task, and then to the raking task immediately afterward. If this was not possible, individuals were exposed to the raking task later in the day or on the next day. This order was kept constant to control for potential transfers of knowledge between tasks.

Data Analysis

We tested 13 individuals from swamp populations (Tripa, Kluet, and Singkil) and 10 individuals from Langkat. We compared the two groups according to their age, time spent in the center, effective time, and possible time via independent Mann-Whitney U tests. We compared their results in the two tasks with Fisher's exact tests because of the small sample size. To explore whether results in the raking task or orangutan characteristics (origin, age, sex, time spent in the center) could predict results in the honey-dipping task, we ran a mixed model analysis, with the results of the honey-dipping task as the dependent variable coded as a binomial response, the results of the raking task and the origin and sex of subjects as fixed factors, and current age and age of arrival at the center as random factors. The model fitted with a binomial error structure. Assumptions of the model were accounted for: the results of the 23 individuals were independent from each other and representative of the populations from which they originated, the homogeneity of error variance was controlled for (Levene's test, LS = 1.601, df1 = 1, df2 = 21, p = 0.220), all variables were tested for significant collinearity, and the residuals were examined for violations of the underlying model assumptions (normality: Shapiro-Wilk's test, W = 0.953, df = 23, p = 0.335).

In a second, larger analysis of honey-dipping and raking knowledge distribution, we included all individuals (n = 30) that could be assigned to either the left bank or the right bank of the Alas River. This analysis was conducted including populations for which extractive tool use has not yet been studied in the wild, but for which tool use can be predicted according to a geographic cultural hypothesis. We analyzed the repartition of knowledgeable and ignorant individuals for both tasks using Fisher's exact tests. All statistics were two sided and calculated with SPSS version 19.

For further information on protocols and data analysis, see Supplemental Experimental Procedures.

Supplemental Information

Supplemental Information includes two figures and Supplemental Experimental Procedures and can be found with this article online at http://dx.doi.org/10.1016/j.cub.2012.09.041.

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